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Temporal changes in the structure of the suprabenthic community from Hendaya beach (southern Bay of Biscay): A comparison with a northwestern Mediterranean beach community

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ABSTRACT

In 1991-1992, the suprabenthic communities from Hendaya and Creixell beaches (southeastern bay of Biscay and northwestern Mediterranean, respectively) were monthly sampled in order to analyse and compare their qualitative and quantitative structural evolution during an annual cycle. The suprabenthos of Hendaya and Creixell beaches shows a similarity rate of 33.3 % for genera and 11.8 % at the species level, mainly amphipods and mysids. The presence of vicariant especies, especially of the genera *Schistomysis*, *Cumposis* and *Eurydice* indicates a certain degree of biogeographical isolation between the suprabenthos of dissipative type beaches from southeastern Bay of Biscay to northwestern Mediterranean.

Key words: Suprabenthos, beach, Bay of Biscay, Mediterranean Sea.

RESUMEN

Cambios temporales en la estructura de la comunidad suprabentónica de la playa de Hendaya (sudeste del golfo de Vizcaya): comparación con la comunidad de una playa del noroeste del Mediterráneo

Las comunidades suprabentónicas de las playas de Hendaya y Creixell (sudeste del golfo de Vizcaya y noroeste del Mediterráneo, respectivamente) han sido mensualmente muestreadas con el objetivo de analizar y comparar su evolución estructural (cualitativa y cuantitativa) durante el ciclo anual 1991-1992. En el suprabentos de las playas de Hendaya y Creixell se han detectado un 33,3 % de géneros y un 11,8 % de especies comunes, principalmente, anfípodos y misidáceos. La presencia de especies vicariantes de los géneros Schistomysis, Cumposis *y* Eurydice, *cuyas respectivas poblaciones son abundantes en ambas playas, revela cierto grado de aislamiento biogeográfico que puede ser, hasta cierto punto, extrapolable al suprabentos de las playas de tipo disipativo localizadas entre la zona sur del golfo de Vizcaya y el noroeste del Mediterráneo.*

Palabras clave: *Suprabentos, playa, golfo de Vizcaya, Mediterráneo.*

INTRODUCTION

Beaches are particularly well suited for biodiversity, dynamic and biogeographical studies, due to their relative accessibility and wide presence along the coast lines. Although sandy beaches dominate most of the European coastlines, where they are subject to ever-increasing pressures from recreational activities, few studies have been carried out on their suprabenthic communities (Suau and Vives, 1957; Moran, 1972; Macquart-Moulin, 1977; Munilla and Corrales, 1995; Munilla, Corrales and San Vicente, 1998).

Suprabenthic crustaceans have been recognised as inhabitants of sandy beaches were they are often highly abundant (Fishelson and Loya, 1968; Wooldridge, 1983). These crustaceans are known to play an important role in nutrient regeneration in the surf zone (Cockroft, Webb and Woolridge, 1988) and are also considered as a major food resource for some fishes and birds (Moran and Fishelson, 1971; Arntz, 1980; Lasiak, 1983; McDermott, 1983; McLachlan, 1983; Modlin and Dardeau, 1987). Most changes in the structure of sandy beaches suprabenthic communities appear to result from the physical changes in wave action and turbulence associated with winds and temperature (Brown and McLachlan, 1990). These changes are important; therefore, sampling should be undertaken during the different environmental condition cycles of the year.

In 1991-1992 a simultaneous study was carried out on the suprabenthic communities from a northwestern Mediterranean beach and a southeastern Bay of Biscay beach, using the same methodology. The results of the Mediterranean beach monitoring have already been presented by San Vicente and Sorbe (1993a; 1999). The present paper deals with observations on the suprabenthic community from Hendaya beach, gathered during one annual cycle in order to describe its qualitative and quantitative structure, the seasonal changes that occurred during that period and, finally, to compare its structure with that (previously studied) of the Mediterranean community. Thus, this approach aims to provide an overall view of the interacting biodiversity, dynamic and biogeographical trends of the suprabenthos from the Atlantic and the Mediterranean beaches.

MATERIAL AND METHODS

Data were monthly collected from a sampling station located within the swash-zone of Hendaya beach (figure 1). A detailed description of this exposed and dissipative-type beach was given by San Vicente (1996). The station is situated in a hydrodynamically controlled environment on sandy sed-

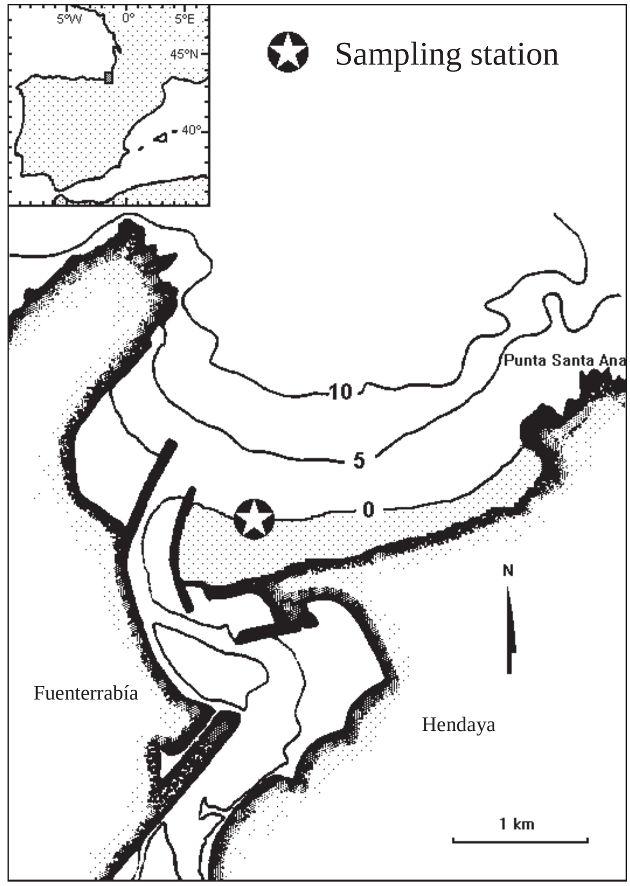


Figure 1. Location of the standard sampling station in the swash zone of Hendaya beach (southeast Bay of Biscay) (isobahts in m)

iments characterised by a mean grain size of 0.195 mm and a low silt-clay content (< 0.5 %). In 1991-1992, the water temperature in the swash-zone fluctuated between 11.0 °C and 24.5 °C, with an annual mean of 15.8 ± 2.4 °C ($\overline{X}$ ± CI 95 %).

Quantitative samples were collected with a suprabenthic sled 50 cm wide and 20 cm high, designed to skim over the surface of the sediment in order to collect the swimming fauna within the 0-20 cm near-bottom water layer (San Vicente and Sorbe, 1993a, b). This sled was equipped with a 0.5 mm mesh net. Tows were undertaken by a single operator wading the swash zone parallel to the shoreline. Samples were collected once a month, during daytime, from February 1991 to February 1992; each sampling session started 1 hour before low-water tide and was completed in about 2 hours. Each month, 10 short successive tows (each 10 m long) and one tow lasting for 100 metre were carried out, providing a satisfactory estimate of the total number of species in the sampled zone (San Vicente and Sorbe, 1993a).

In order to complete the information provided by the standard sampling station, further samples were taken in September 1991, following the same method used at the standard sampling zone: day-time samples at depths of 6 and 10 m, using scuba-diving, as well as night-time low-tide and diurnal high-tide swash zone samples.

Data analysis followed the scheme proposed by Field, Clarke and Warwick (1982). 'Root-root' transformed abundance values were used to construct a Bray-Curtis dissimilarity matrix. Classification was performed with the complete linkage clustering technique whereas ordination (non-metric multidimensional scaling MDS) was used to evaluate the group separation derived from cluster analysis (Clarke, 1993; Clarke and Warwick, 1994).

RESULTS

Species composition and resident populations

Species list is shown on table I.

Table I. Species list

MYSIDACEA
Siriella armata (Milne-Edwards, 1837)
Anchialina agilis (G. O. Sars, 1877)
Gastrosaccus roscoffensis Bacescu, 1970
Gastrosaccus sanctus (Van Beneden, 1861)
Gastrosaccus spinifer (Goes, 1864)
Mysidopsis gibbosa G. O. Sars, 1864
Acanthomysis longicornis (Milne-Edwards, 1837)
Mesopodopsis slabberi (Van Beneden, 1861)
Paramysis bacescoi Labat, 1953
Paramysis arenosa (G. O. Sars, 1877)
Schistomysis parkeri Norman, 1892
Schistomysis spiritus (Norman, 1860)
AMPHIPODA
Ampelisca brevicornis (Costa, 1853)
Stenothoe monoculoides (Montagu, 1815)
Bathyporeia nana Toulmond, 1966
Bathyporeia pilosa Lindström, 1855
Urothoe elegans (Bate, 1856)
Perioculodes longimanus (Bate & Westwood, 1868)
Pontocrates altamarinus (Bate & Westwood, 1858)
Pontocrates arenarius (Bate, 1858)
Megaluropus agilis Hoek, 1889
Apherusa bispinosa (Bate, 1856)
Apherusa jurinei (Milne-Edwards, 1830)
Atylus swammerdami (Milne-Edwards, 1830)
Dexamine spinosa (Montagu, 1813)
Dexamine thea Boeck, 1861
Guernea coalita (Norman, 1868)
Microprotopus maculatus Norman, 1867

Table I (continued)

AMPHIPODA
Corophium acutum Chevreux, 1908
Siphonoecetes kroyeranus Bate, 1856
Jassa marmorata Holmes, 1903
CUMACEA
Eocuma dollfusi Calman, 1907
Iphinoe trispinosa (Goodsir, 1843)
Cumopsis fagei Bacescu, 1956
Nannastacus unguiculatus (Bate, 1859)
Pseudocuma longicornis (Bate, 1858)
ISOPODA
Dynamene bidentata (Adams, 1852)
Sphaeroma serratum (Fabricius, 1798)
Eurydice pulchra Leach, 1815
EUPHAUSIACEA
Nyctiphanes couchi (Bell, 1853)
DECAPODA
Hippolyte leptocerus (Heller, 1863)
Palaemon elegans Rathke, 1837
Crangon crangon (Linnaeus, 1758)
Philocheras bispinosus (Hailstone, 1835)
Philocheras trispinosus (Hailstone, 1835)
Callianassa subterranea (Montagu, 1808)
Anapagurus hyndmanni (Bell, 1846)
Galathea squamifera Leach, 1814
Porcelana platycheles (Pennant, 1777)
Portumnus latipes (Pennant, 1777)

During the 1991-1992 monitoring survey, a total of 45 suprabenthic taxa belonging to 9 taxonomic groups (Pycnogonida, Leptostraca, Mysidacea, Amphipoda, Cumacea, Tanaidacea, Isopoda, Euphausiacea and Decapoda Natantia) were recorded in the standard sampling station of Hendaya beach (table II). Mega-epibenthic organisms (e.g., demersal fish, adult crabs, etc.), as well as true planktonic animals (e.g., Calanoida), were excluded from the analysis.

Within this collected material, four species continuously occupied the swash zone of Hendaya beach and were considered as resident organisms (frequency of occurrence: 100 %): the mysids *Schistomysis parkeri*, *Gastrosaccus roscoffensis*, the amphipod *Pontocrates arenarius* and the cumacean *Cumopsis fagei*. Two species had a frequency of occurrence higher than 50 %: *Eurydice pulchra* (76.9 %) and *Philocheras trispinosus* (53.8 %). The further 39 taxa were sporadically found through the year with a frequency of occurrence less than 50 %.

Table II. Annual mean densities ($\bar{X}$: indiv/5 m² ± CI 95 %) and residence (R, presence in monthly samples; total number of samples: 13) of suprabenthic taxa within the standard sampling zone of Hendaya beach during 1991-1992. (*): species contributing more than 1 % of total abundance in any sample of the standard zone and selected for classification and ordination techniques

Taxa	$\bar{X}$	± CI 95	R	Taxa	$\bar{X}$	± CI 95	R
PYCNOGONIDA				CUMACEA (cont.)			
Unidentified	0.01	0.06	1	*Eocuma dollfusi*	0.04	0.35	4
LEPTOSTRACA				*Nannastacus unguiculatus*	0.01	0.25	2
Nebalia sp.	0.01	0.06	1	*Cumella* sp.	0.08	0.32	3
MYSIDACEA				TANAIDACEA			
Siriella sp.	0.20	0.23	2	Unidentified	0.01	0.18	1
Gastrosaccus roscoffensis *	4.18	3.64	13	ISOPODA			
Gastrosaccus sanctus	0.09	0.34	4	*Dynamene bidentata*	0.02	0.25	2
Gastrosaccus spinifer	0.08	0.40	6	*Sphaeroma serratum* *	0.08	0.19	1
Paramysis bacescoi *	0.12	0.26	2	*Eurydice pulchra* *	2.48	3.24	9
Schistomysis parkeri *	59.79	73.62	13	*Gnathia* sp.	0.02	0.18	1
Schistomysis spiritus *	0.12	0.19	3	EUPHAUSIACEA			
Mesopodopsis slabberi *	0.19	0.42	2	*Nyctiphanes couchi* (calyptopis)	0.04	0.31	3
AMPHIPODA				DECAPODA			
Stenothoe monoculoides	0.02	0.18	1	*Hippolyte leptocerus*	0.01	0.18	1
Bathyporeia sp. *	0.22	0.26	5	Hippolytidae (zoea II)	0.01	0.18	1
Perioculodes longimanus	0.01	0.18	1	Alpheidae (juvenile)	0.03	0.25	2
Pontocrates altamarinus *	0.08	0.14	4	*Palaemon elegans* (juvenile)	0.14	0.35	3
Pontocrates arenarius *	2.41	1.12	13	*Crangon crangon*	0.03	0.25	2
Apherusa jurinei	0.01	0.18	1	*Philocheras bispinosus* (zoea)	0.01	0.18	1
Atylus swammerdami	0.07	0.39	5	*Philocheras trispinosus* *	0.86	1.33	7
Guernea coalita *	0.11	0.14	4	*Anapagurus hyndmanni* (megalopa)	0.13	0.42	5
Corophium sp.	0.01	0.18	1	*Galathea squamifera* (zoea)	0.01	0.18	1
Jassa marmorata	0.02	0.25	2	*Porcelana platycheles* (megalopa)	0.03	0.30	3
Caprellidea	0.01	0.18	1	Brachyura (megalopa) *	1.21	2.00	6
CUMACEA				*Portumnus latipes* (juvenile)	0.05	0.31	3
Cumopsis fagei *	15.47	14.03	13	Portunidae (juvenile)	0.02	0.30	3
Iphinoe sp.	0.01	0.18	1				

Bathymetric distribution and nycthemeral and tidal migrations

Complementary samples taken in September 1991 at depths of 6 and 10 m revealed the existence of another community, characterised by the dominance of the mysids *Mesopodopsis slabberi* and *Acanthomysis longicornis*, the amphipods *Megaluropus agilis* and *Microprotopus maculatus* and the cumacean *Pseudocuma longicornis*. Except *M. slabberi*, the other four species were never found at the standard station sampled during 1991-1992. Furthermore, the following species found at depths of 6 and 10 m were never collected at the standard station: the mysids *Siriella armata*, *Paramysis arenosa*, *Mysidopsis gibbosa* and *Anchialina agilis* and the amphipods *Apherusa bispinosa*, *Dexamine spinosa*, *D. thea*, *Siphonoecetes kroyeranus*, *Bathyporeia pilosa*, *B. nana*, *Ampelisca brevicornis*, *Megaluropus agilis*, *Microprotopus maculatus* and *Urothoe elegans* and the decapod *Callianassa subterranea* (table III).

During the night (low-tide), the swash zone suprabenthic community of Hendaya beach was characterized by higher abundances of the resident species *G. roscoffensis*, *C. fagei* and *E. pulchra* and minor changes in the presence and density of the other populations (table III).

The comparison of the swash zone community structure at low and high tides showed that tidal migrations did occur on this beach. The mysid *Schistomysis parkeri* performed a tidal migration during the day, moving upshore with flood tide and reaching its highest abundance value in the swash zone at high tide. The mysids *Mesopodopsis slabberi* and *Schistomysis spiritus* also reached their highest densities in the swash zone at high tide. The other suprabenthic species that occurred at the standard sampling station did not move upshore with the tide.

Table III. Mean densities ($\bar{X}$: indiv/5 m^2 ± CI 95 %) of suprabenthic taxa sampled at Hendaya beach in September 1991. Diurnal and nocturnal low-tide samples in the standard swash zone, high-tide samples in the swash zone and daytime samples taken at depths of 6 and 10 m using scuba. Selected species representing more than 0.1 indiv/5 m^2 in any sample. (PYC): Pycnogonida; (MYS): Mysidacea; (AMP): Amphipoda; (CUM): Cumacea; (ISO): Isopoda; (DEC): Decapoda

Bathymetric zone		Swash						-6 m	-10m
Day/night		Day		Night		Day		Day	Day
High/low tide		low tide		low tide		high tide			
		$\bar{X}$ ± CI 95		$\bar{X}$ ± CI 95		$\bar{X}$ ± CI 95		indiv/5 m^2	indiv/5 m^2
PYC	Pycnogonida unidentified	—	—	—	—	—	—	0.2	—
MYS	*Siriella armata*	—	—	—	—	—	—	0.2	—
MYS	*Gastrosaccus roscoffensis*	7.5	5.1	16.8	17.4	—	—	—	—
MYS	*Gastrosaccus sanctus*	0.1	0.2	—	—	0.2	0.2	1.5	1.2
MYS	*Gastrosaccus spinifer*	0.1	0.2	0.2	0.6	—	—	—	—
MYS	*Anchialina agilis*	—	—	—	—	—	—	—	0.1
MYS	*Mysidopsis gibbosa*	—	—	—	—	—	—	—	0.1
MYS	*Paramysis bacescoi*	—	—	0.6	1.7	—	—	1.3	2.4
MYS	*Paramysis arenosa*	—	—	—	—	—	—	0.3	0.7
MYS	*Schistomysis parkeri*	64.3	46.8	67.8	88.2	102.6	77.5	—	0.3
MYS	*Schistomysis spiritus*	—	—	—	—	27.4	22.3	—	—
MYS	*Mesopodopsis slabberi*	—	—	—	—	32.2	21.6	26.3	4.0
MYS	*Acanthomysis longicornis*	—	—	—	—	0.2	0.2	1.5	13.9
AMP	*Ampelisca brevicornis*	—	—	—	—	—	—	—	0.1
AMP	*Bathyporeia pilosa*	—	—	—	—	—	—	0.5	—
AMP	*Bathyporeia nana*	—	—	—	—	—	—	1.1	—
AMP	*Bathyporeia* sp.	—	—	0.8	1.6	—	—	—	6.1
AMP	*Urothoe elegans*	—	—	—	—	—	—	—	0.1
AMP	*Perioculodes longimanus*	—	—	—	—	—	—	—	0.8
AMP	*Pontocrates altamarinus*	0.1	0.2	0.2	0.6	—	—	—	—
AMP	*Pontocrates arenarius*	0.8	0.6	0.8	1.6	0.2	0.2	2.7	6.8
AMP	*Megaluropus agilis*	—	—	—	—	—	—	5.7	7.1
AMP	*Apherusa bispinosa*	—	—	—	—	—	—	0.2	—
AMP	*Atylus swammerdami*	—	—	—	—	—	—	3.8	0.2
AMP	*Dexamine spinosa*	—	—	—	—	—	—	0.2	—
AMP	*Dexamine thea*	—	—	—	—	—	—	0.3	—
AMP	*Guernea coalita*	—	—	0.2	0.6	—	—	—	—
AMP	*Microprotopus maculatus*	—	—	—	—	—	—	9.0	0.5
AMP	*Corophium acutum*	—	—	0.2	0.6	—	—	—	—
AMP	*Siphonoecetes kroyeranus*	—	—	—	—	—	—	0.3	0.1
CUM	*Cumopsis fagei*	12.6	10.4	45.0	69.9	—	—	—	0.2
CUM	*Bodotria* sp.	—	—	—	—	—	—	—	0.2
CUM	*Iphinoe trispinosa*	—	—	0.2	0.6	—	—	0.1	0.1
CUM	*Pseudocuma longicornis.*	—	—	—	—	0.2	0.5	8.5	16.7
CUM	*Eocuma dollfusi*	0.1	0.2	0.2	0.6	—	—	—	—
ISO	*Eurydice pulchra*	—	—	6.8	6.1	0.2	0.5	—	—
ISO	*Sphaeroma serratum*	—	—	0.6	0.7	—	—	—	—
DEC	*Hippolyte leptocerus*	—	—	—	—	—	—	0.3	—
DEC	*Palaemon elegans* (juvenile)	0.4	0.3	0.2	0.6	—	—	—	—
DEC	*Philocheras trispinosus*	7.8	4.3	—	—	—	—	0.7	0.3
DEC	*Callianassa subterranea* (juvenile)	—	—	—	—	—	—	0.2	—
DEC	*Anapagurus hyndmanni* (megalopa)	0.8	0.8		—	—	—	0.9	0.7
DEC	Brachyura (megalopa)	1.1	2.2	0.4	0.7	—	—	0.9	0.4
DEC	*Portumnus latipes* (juvenile)	0.5	0.6	0.4	1.1	—	—	—	—
DEC	Portunidae (juvenile)	—	—	—	—	—	—	—	0.3
	TOTAL	96.2	56.8	141.4	71.2	163.2	101.1	66.7	63.4

Density evolution and diversity

The mean suprabenthos abundance from the standard sampled station of Hendaya beach ranged between a maximum of 488.4 indiv/5 m^2 in July 1991 and a minimum of 25.4 indiv/5 m^2 in December 1991 (annual mean = 88.3 ± 77.5 indiv/5 m^2; $\bar{X}$ ± CI 95 %) (table IV).

The highest diversity value (H´ = 2.5) was observed in October as a result of a more even abundance distribution of the species found in this sample. Despite the relative high species richness of the sample, the lowest diversity value (H´ = 0.7) was observed during July 1991 due to the dominance of *S. parkeri* (table IV).

As shown by figure 2, the classification of the 13 monthly samples from the standard station showed that samples could be grouped into three main clusters A, B1 and B2. Although agreement with the cluster analysis was good, the corresponding ordination (figure 3) revealed a gradient of change from winter months (group A: few species and lower densities) to spring (group B1: median values) and summer (group B2: higher number of species and higher densities). The October sample was clearly separated from the others due to its higher diversity value and different dominant species.

Fourteen species, all contributing more than 1 % of the total abundance in any sample at the standard sampling station, were selected for further faunistical analysis (98.9 % of the total number of specimens collected during 1991-1992). Listed in table IV with their monthly abundances and annual mean values, these selected species were classi-

Table IV. Monthly density evolution (mean values) and annual mean density (indiv/5 m²) of the 14 dominant suprabenthic species (selected species representing more than 1 % of total abundance in any sample of the standard zone). Total density (mean values; indiv/5 m²); species richness S and diversity (Shannon index H') of the suprabenthic community sampled at the standard station of the Hendaya beach during 1991-1992

	F91	M	A	M	J	J	A	S	O	N	D	J92	F	$\bar{X}$ ± CI 95	
Gastrosaccus roscoffensis	0.4	0.1	0.2	0.1	0.3	15.4	0.7	7.5	16.0	7.7	0.6	4.2	1.1	4.18	3.64
Paramysis bacescoi	—	—	—	—	—	—	1.5	—	—	—	0.1	—	—	0.12	0.26
Schistomysis parkeri	11.3	54.3	27.0	28.3	11.0	442.9	69.2	64.3	6.1	14.4	15.2	19.8	13.5	59.79	73.62
Schistomysis spiritus	—	—	—	0.1	—	—	0.3	—	1.1	—	—	—	—	0.12	0.19
Mesopodopsis slabberi	—	—	—	—	—	—	0.1	—	2.4	—	—	—	—	0.19	0.42
Bathyporeia sp.	—	0.1	—	—	0.8	0.3	0.4	—	—	1.3	—	—	—	0.22	0.26
Pontocrates altamarinus	—	—	—	—	—	0.1	0.1	0.1	0.8	—	—	—	—	0.08	0.14
Pontocrates arenarius	1.7	0.7	2.8	0.8	5.5	2.5	1.8	0.8	0.5	2.1	3.8	2.2	6.1	2.41	1.12
Guernea coalita		0.6					0.1		0.6				0.1	0.11	0.14
Cumopsis fagei	2.2	18.7	9.2	5.7	87.1	22.5	3.2	12.6	10.1	5.5	5.6	7.6	11.1	15.47	14.03
Sphaeroma serratum	—	—	—	—	—	—	1.1	—	—	—	—	—	—	0.08	0.19
Eurydice pulchra	18.4	0.3	0.1	—	0.1	1.8	—	—	0.3	5.7	—	0.7	4.8	2.48	3.24
Philocheras trispinosus	—	0.6	—	0.1	0.9	0.2	0.6	7.8	1.0	—	—	—	—	0.86	1.33
Brachyura (megalopa)	—	0.1	0.2	11.5	—	0.2	2.6	1.1	—	—	—	—	—	1.21	2.00
Total density	34.3	77.1	39.6	47.4	107.5	488.4	83.7	96.4	40.1	36.7	25.4	34.5	37.1	88.32	77.48
CI 95%	12.7	60.8	22.4	26.5	121.9	144.0	32.1	59.9	26.4	18.9	10.9	16.3	6.7		
S (cumulative)	7	16	7	14	13	22	25	15	17	6	6	5	9	12.46	4.07
H' (log_2)	1.6	1.3	1.3	1.6	1.1	0.7	1.3	1.7	2.5	2.2	1.5	1.7	2.1	1.58	0.30

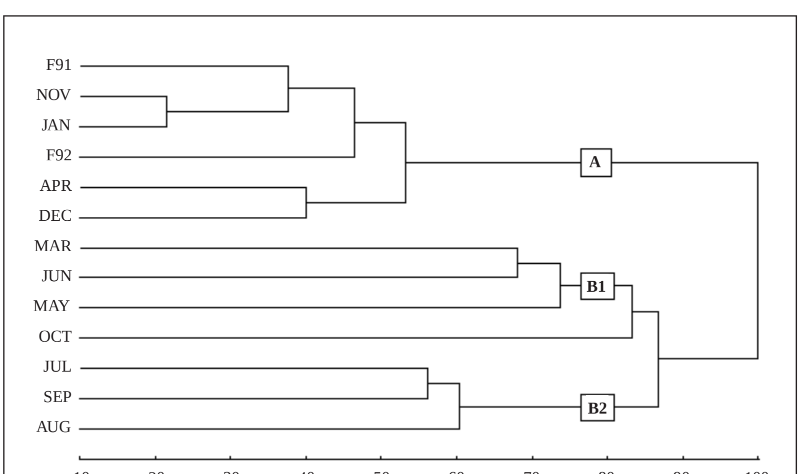
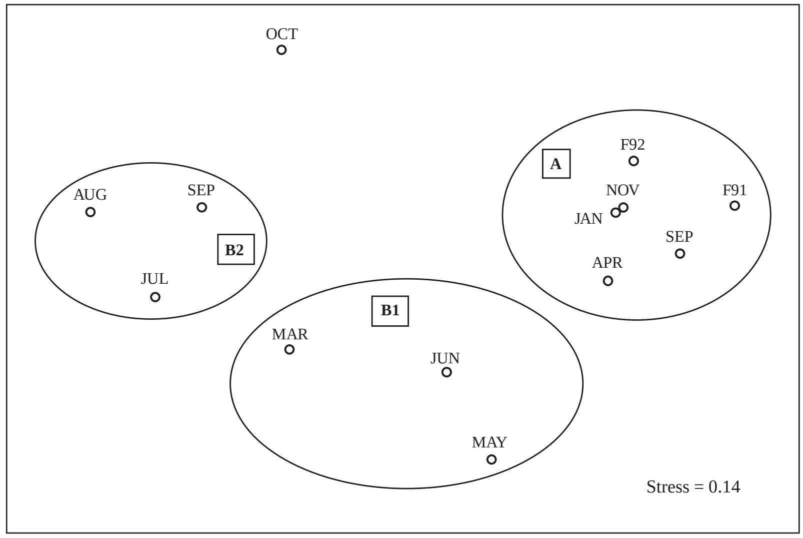


Figure 2. Cluster analysis showing the classification of the 13 monthly samples from the Hendaya standard station. Species abundances were standardized and compared using the Bray-Curtis dissimilarity index and complete linkage method of sorting

Figure 3. MDS ordination of the 13 monthly samples from the Hendaya standard station in 1991-1992. Bray-Curtis dissimilarity measures calculated on the basis of standardized abundances. Stress: <0.05 = excellent representation, <0.1 = good, <0.2 = still useful, >0.2 = difficult to interpret



fied into four species groups based on the dendogram of hierarchical classification of dissimilarities between species (figure 4). These groups can be associated with the residence time and the monthly abundance fluctuations of species, as also demonstrated by MDS analysis (figure 5).

Group 1 included the resident and dominant species of the swash zone community in the annual cycle: *S. parkeri*, *C. fagei*, *E. pulchra, G. roscoffensis* and *P. arenarius.* All of them are characteristic components of the swash-zone suprabenthic community, representing 95.5 % of the total of individuals collected in 1991-1992 and with a frequency of occurrence higher than 69 %. The maximum density of *S. parkeri*, *G. roscoffensis*, *P. arenarius* and *C. fagei* was recorded in late spring and early summer. Group 2 included three taxa (2.6 % of the total abundance in 1991-1992) that were absent at the standard station during the winter months: Brachyura (megalopa), *Philocheras trispinosus* and *Bathyporeia* sp. Group 3 included non resident species representing only 0.2 % of the total abundance and mainly detected at the standard station in August (*P. bacescoi* and *Sphaeroma serratum*). Finally, group 4 consists of non resident species representing only 0.6 % of the total abundance and sporadically sampled at the standard zone during the year: *M. slabberi*, *S. spiritus*, *P. altamarinus* and *Guernea coalita.*

Hendaya and Creixell community comparison

Table V shows the main environmental data and the basic suprabenthic community variables of Hendaya beach (this study) and Creixell beach

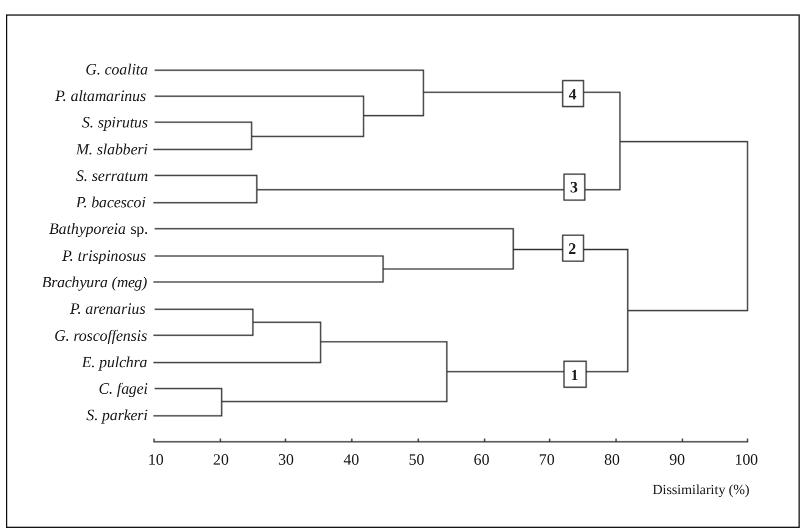


Figure 4. Cluster analysis showing the classification of the 14 selected species contributing more than 1 % of total abundance in any 1991-1992 sample from the Hendaya standard station. Bray-Curtis dissimilarity index and complete linkage method of sorting

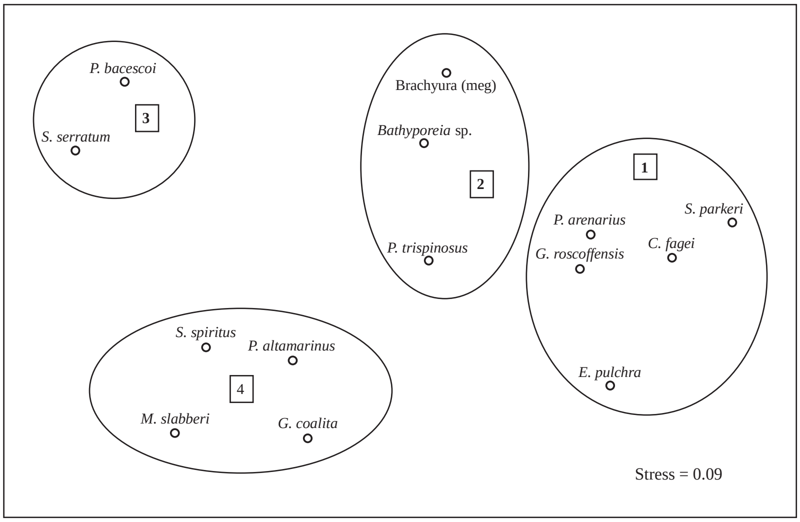


Figure 5. MDS ordination of the 14 selected species contributing more than 1 % of total abundance in any 1991-1992 sample from the Hendaya standard station. Bray-Curtis dissimilarity measures calculated on the basis of standardized abundances. (meg): megalopa. Stress: <0.05 = excellent representation, <0.1 = good, <0.2 = still useful, >0.2 = difficult to interpret

(San Vicente and Sorbe, 1999) during the 1991-1992 annual cycle. Both are exposed and dissipative-type beaches, with hydrodynamically controlled environments, fine sandy sediments and low silt-clay content. The water temperature range was slightly higher at Creixell beach than at Hendaya beach, with a difference of about 2 °C between their respective annual means. Furthermore, the compared Mediterranean and Atlantic beaches also featured notable differences regarding their tidal characteristics and subsequent degree of exposure.

Table V. Main environmental and suprabenthic community structure parameters of Hendaya beach (this study) and Creixell beach (San Vicente and Sorbe, 1999) during 1991-1992 (+: traces, not measured)

	Hendaya beach	Creixell beach
Environmental variables		
Water temperature (°C)		
Range	11.0 - 24.5	12.4 - 26.1
Mean ($\bar{X}$ ± CI 95 %)	15.8 ± 2.4	17.2 ± 2.9
Sediment		
Mean grain size (mm)	0.195	0.185
Fine sand (%)	74.8	84.5
Silt-clay content (%)	<0.5	<0.5
Detritic fraction (mg AFDW/5 m^2)		
Range	+	11.4 - 578.1
Mean ($\bar{X}$ ± CI 95 %)	+	180.8 ± 73.8
Community structure		
Species richness (cumulative)	45	97
Nº of resident taxa	4	11
Diversity (H': log_2)		
Range	0.7 - 2.5	1.6 - 3.4
Mean	1.6	2.5
Density (indiv/5 m^2)		
Range	25 - 488	13 - 280
Mean	88	94
Seasonal maximum	Summer	Spring
Seasonal minimum	Autumn	Autumn

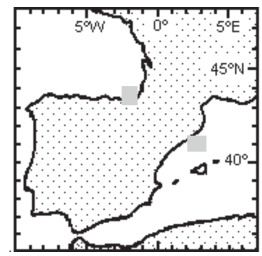
As shown in table V, the Creixell community exhibited a higher species richness (S = 97), diversity value (H' = 2.5) and percentage of resident taxa (11.3 %) than the Hendaya community (S = 45; H' = 1.6; resident taxa = 8.9 %).

The range of monthly abundance values recorded in each sampling area was significantly larger in the case of the Hendaya community, but the mean density values were within the same order of magnitude. However, the maximum density values were recorded at different periods of the year: in spring for the Hendaya community, in summer for the Creixell one. In both communities, the minimum density values were observed in autumn.

Twenty-two genera and thirteen species were common to both beaches (33.3 % and 11.8 % of the total number of genera and species, respectively) (figure 6). Amphipoda and Mysidacea were the main groups that contributed to the faunistical similarity between beaches. On the other hand, eleven genera were represented by vicariant species on the two beaches studied, some of them very abundant in their respective beach community (*Cumopsis*, *Schistomysis* and *Eurydice*).

Contributing more than 2 % of total abundance in any sample from each beach community, twenty especies were selected for further faunistical comparison (96.5 % and 98.8 % of total number of specimens collected in 1991-1992 at Creixell and

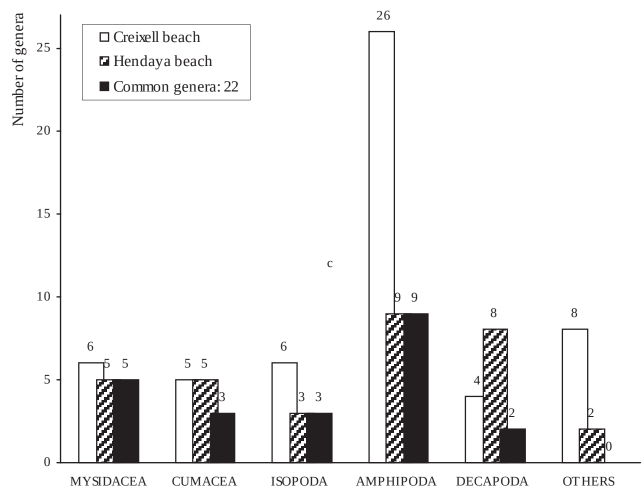
ANNUAL CYCLE 1991-1992



Hendaya and Creixell beaches

Common genera

MYSIDACEA
Siriella
Paramysis
Gastrosaccus
Schistomysis
Mesopodopsis
AMPHIPODA
Apherusa
Corophium
Guernea
Periocul odes
Bathyporeia
Jassa
Stenothoe
Atylus
Pontocrates
CUMACEA
Cumella
Iphinoe
Cumopsis
ISOPODA
Dynamene
Sphaeroma
Eurydice
DECAPODA
Palaemon
Philocheras



Common species

MYSIDACEA
Gastrosaccus spinifer
Gastrosaccus sanctus
Gastrosaccus roscoffensis
Mesopodopsis slabberi
AMPHIPODA
Guernea coalita
Jassa marmorata
Pontocrates altamarinus
Pontocrates arenarius
Stenothoe monoculoides
Atylus swammerdami
ISOPODA
Dynamene bidentata
Sphaeroma serratum
DECAPODA
Philocheras trispinosus

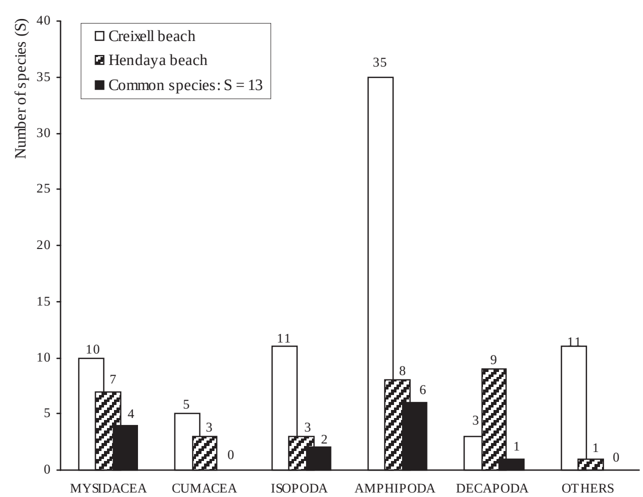


Figure 6. Common suprabenthic genera and species recorded during the simultaneous 1991-1992 study of Hendaya and Creixell beaches

Hendaya beaches, respectively). These selected species were classified into four major species groups (C1, C2, H1 and H2) (figure 7) using their frequency of occurrence and abundance pattern within the beach communities, as also depicted by the MDS analysis (figure 8).

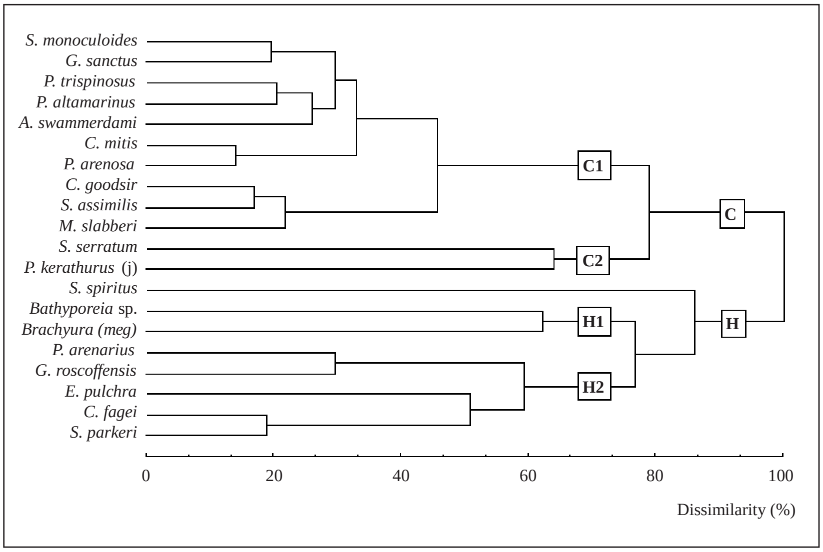


Figure 7. Cluster analysis showing the classification of the 20 selected species contributing more than 2 % of total abundance in any 1991-1992 sample from Hendaya and Creixell standard stations. Bray-Curtis dissimilarity index and complete linkage method of sorting. (j): juvenile; (meg): megalopa

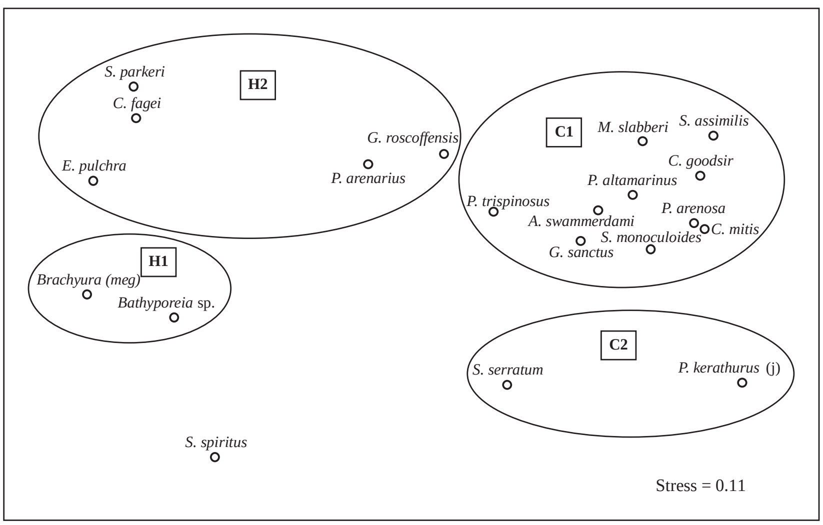


Figure 8. MDS ordination of the 20 selected species contributing more than 2 % of total abundance in any 1991-1992 sample from Hendaya and Creixell standard stations. Bray-Curtis dissimilarity measures calculated on the basis of standardized abundances. (j): juvenile; (meg): megalopa. Stress: <0.05 = excellent representation, <0.1 = good, <0.2 = still useful, >0.2 = difficult to interpret

Group C1 included the dominant species of the Creixell community, representing 92.9% of its total annual abundance. Four of these species were found exclusively at Creixell beach and represented 44.5 % of the total abundance (*Cumopsis goodsir*, *Schistomysis assimilis*, *Caprella mitis* and *Paramysis arenosa*). The other six species of this group (*Stenothoe monoculoides*, *Gastrosaccus sanctus*, *Philocheras trispinosus*, *Pontocrates altamarinus*, *Atylus swammerdami* and *Mesopodopsis slabberi*) were found at both beaches, although with higher abundances at Creixell beach (47.9 % of total abundance at Creixell beach and only 1.6 % of at Hendaya beach). Group C2 included two species *S. serratum* and *Penaeus kerathurus* (juvenile). Both species mainly appeared at Creixell beach during spring and summer and *S. serratum* were only detected in August at Hendaya beach. Group H1 gathered unidentified brachyuran megalopa collected at Hendaya beach and *Bathyporeia* sp. more abundant on Hendaya beach than on Creixell beach.

Group H2 included the five dominant species of the Hendaya community, representing 95.5 % of its total abundance in 1991-1992: *E. pulchra*, *C. fagei*, *S. parkeri*, *P. arenarius* and *G. roscoffensis*. *E. pulchra*, *C. fagei* and *S. parkeri* were exclusively recorded at Hendaya beach and represented 88.0 % of the total annual abundance of this community. *P. arenarius* and *G. roscoffensis* were recorded at both beaches, although with higher densities on Hendaya beach. Finally, *S. spiritus* was classified apart from the other selected species by the cluster and MDS analysis, due to its sporadic presence (May, August and October) in the Hendaya community.

DISCUSSION

Swash-zone characteristics seem to be suitable for the establishment of some abundant suprabenthos populations on exposed sandy beaches. The environment around the swash zone is relatively calm compared to that of the seaward zone, because much of the wave energy is consumed in the surf zone and the momentum of the waves is slackened by friction against the beach face (Flemming and Fricke, 1983; Takahashi and Kawaguchi, 1995). Furthermore, intertidal swash climate implies a seawater sand filtering process related to high nutrient cycling flows (Pugh, 1983; Lord and Eagle, 1983) and its consequent productivity.

Following the tidal changes of the swash-zone position, the mysid *S. parkeri* ranged over nearly all the intertidal zone on Hendaya beach. This behaviour, which has been also described for *Gastrossacus psammodytes* (Wooldridge, 1981, 1983), may be related to optimal maintenance in the feeding zone (Trueman, 1971), to predator avoidance (McLachlan *et al.*, 1979) and to the maintenance in the swash zone, where water coverage is almost continuous but wave action not too severe. Almost all other suprabenthic components of Hendaya beach do not migrate with the tidal swash-backswash movement and probably stay in the resurgence and upper saturation zones of the beach at high tide (Salvat, 1964). *S. spiritus* and *M. slabberi* were exclusively observed in the high tide swash zone in September, thus indicating that a seasonal colonisation of the upper intertidal swash zone may also occur (San Vicente and Sorbe, 1995).

Related to their nycthemeral migratory behaviour between sediment and near-bottom water layer, some populations (like *E. pulchra* and *P. bacescoi*) are diurnally endobenthic and nocturnally suprabenthic components of the Hendaya community. Cirolanid isopods (genus *Eurydice*) and some mysids of the genus *Gastrosaccus* (Dahl, 1952; Salvat, 1964; Peres and Picard, 1964; McLachlan, Cockcroft and Malan, 1984) are known as members of the beach interstitial infauna (Naylor, 1972; Moran, 1972), but their presence in diurnal suprabenthic samples proves that they may exhibit a certain swimming behaviour in the near-bottom water layer. Such a nocturnal swimming behaviour has been described in some cumaceans, mysids, amphipods and decapods (Wang and Dauvin, 1994). The present study confirms these observations and shows that nycthemeral and tidal cycles hardly influences the distribution of beach suprabenthic organisms.

The following features of the Hendaya suprabenthos community are generally encountered on exposed and dissipative sandy beaches: relative faunistic originality, few resident species (mainly crustaceans, because they need to be strong swimmers), high dominance of a few species (specially mysids), high densities and biomasses and finally patchy distributions (Ledoyer, 1966; Brown and McLachlan, 1990). The suprabenthos of Hendaya beach consists almost entirely of crustaceans, dominated by mysids, amphipods, decapods, cumaceans and isopods. Theses taxonomic groups were also dominant in other coastal suprabenthic communities from European coast (Boysen, 1975; Hesthagen, 1973; Kaartvedt, 1985, 1989; Buhl-Jensen, 1986; Buhl-Jensen and Fossa, 1991; Wang and Dauvin, 1994).

The mysids *S. parkeri* and *G. roscoffensis* are resident and dominant components of the Hendaya suprabenthic community. Both species have a vertical distribution exclusively restricted to littoral environment (Bacescu, 1941, 1970; Müller, 1993). Contrary to the findings of Tattersall and Tattersall (1951), who stated that *S. parkeri* inhabits the estuaries, this species has been found neither in estuaries nor at deeper depths of the inner shelf in the southeast Bay of Biscay (Sorbe, 1980; 1984; San Vicente *et. al.*, 1990). Despite its relative high abundance in some of these environments, *S. parkeri* was generally not reported in the literature on European beaches' macrofauna, indicating a lack of attention to such swimming crustaceans in littoral areas.

The non-resident suprabenthos of the Hendaya beach includes a high number of taxa with different origin (e.g., infauna, suprabenthos from deeper depths, meroplankton), whose sporadic presence in the swash zone is related to nyctemeral or seasonal cycles as well as to advection by wind-, wave- and tide-induced currents. Lagardere (1966) mentioned a high diversity of macroinfaunal taxa in the Hendaya beach's benthic community of. The similar biodiversity level observed for its suprabenthos could be related to a high degree of competence and mixing of swimming animals from different biotopes (Picard, 1965).

Fourteen taxa of a suprabenthic community described by Sorbe (1984) at a depth of 30 m (in front of Arcachon Bay) were also sampled in

Hendaya beach's swash zone. Five of them had also been reported in the neighbouring Bidasoa estuary (San Vicente, Guzmán and Ibañez, 1990): the mysids *G. spinifer* and *M. slabberi*, the amphipods *P. altamarinus* and *A. swammerdami*, and the decapod *P. trispinosus*. These species have a wide horizontal distribution range on the Atlantic European coasts, from estuaries (Sorbe, 1980; Mees, Cattrijsse and Hamerlynck, 1993; Cattrijsse, Mees and Hamerlynck, 1993) to infralittoral bottoms (Hamerlynck and Mees, 1991; Mess and Hamerlynck, 1992; Mees, 1994) and are able to live in the swash-zone of exposed beaches.

Ibañez (1990) summarized the biogeographical trends of the invertebrate fauna in the southeast Bay of Biscay and western Mediterranean. In the present study, 33.3 % of the genera and 11.8 % of the species (mainly amphipods and mysids) were common to both beaches sampled. These faunistical observations confirm that the northwestern Mediterranean is a biogeographical transition zone between the Atlantic and the eastern Mediterranean zones, in agreement with the available data on Spanish amphipod fauna (Jimeno, 1993) and mysid distribution (mysid boundary in the eastern Atlantic appears to be south of the entrance to the Mediterranean, at about 30º N: Mauchline, 1980).

On the other hand, the presence of vicariant species in several genera (*Schistomysis*, *Cumposis*, *Eurydice*) revealed some degree of biogeographical isolation between littoral communities from the northeastern Atlantic and the northwestern Mediterranean.

In 1991-1992, the suprabenthos of Hendaya beach showed a maximum density in summer and a minimum in autumn. This seasonal density pattern seems to be a typical feature of European Atlantic beaches (Dexter, 1990). In contrast, the seasonal density pattern of the Creixell community is different with maximum values in spring, probably related to distinct trophic conditions in the littoral environments of the northwestern Mediterranean.

Autumn density decay is a common feature of both communities, probably related to mortality and seasonal migration of species to deeper bottoms in order to avoid the stronger hydrodynamic conditions that seasonally prevail in such littoral environments.

Finally, as has also been reported for other beaches (Lasiak, 1983, 1986; Lasiak and McLachlan, 1987; Wooldridge, 1983; McLachlan, 1983; Du Preez *et al.*, 1990), the Hendaya and Creixell beach communities play an important trophic role in coastal environments, due to the relative abundance of some peracarid populations. On such exposed beaches, a few resident populations are responsible of most of the global secondary production (Brown and McLachlan, 1990). This production is consumed by some fishes (e.g., Mugilidae and Pleuronectiforma), which were observed at Hendaya and Creixell beaches in 1991-1992. Furthermore, the swimming behaviour of suprabenthos and their predators probably contributes to the exportation of a more or less important part of the secondary production from the beach environment to deeper bottoms.

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